Syo KUROKAWA*: **Chemical variation in the *Parmelia physcioides* group (Lichenes)**

黒川 逍*: *Parmelia physcioides* 群における二次代謝産物の変異

(Plate III)

Parmelia physcioides Nyl. belongs to section Hypotrachyna, one of eight sections of *Parmelia* subgenus Parmelia (Hale & Kurokawa 1964). The section Hypotrachyna contains approximately 120 species, most of which are subtropical, montane-tropical, or temperate. Eighteen of them, including *P. physcioides*, produce atranorin and barbatic acid accompanied by one or more of five secondary products of known constitution. Four species, *P. chlorina* Müll.-Arg., *P. endochlora* Tayl., *P. isidiocera* Nyl., and *P. peruviana* Nyl., have pale yellow medulla due to the presence of the yellow pigment, entothein (=secalonic acid A), and are considered to form a separate group. *P. moniliifera* Kurok. is also quite distinctive, having a divaricate thallus with linear-elongate lobes and has unusual moniliform rhizines. It does not seem to be related to the other barbatic acid producing species. These five species are not included in the present study. The remaining 13 species have similar adnate to loosely adnate thalli with sublinear lobes and moderately branched rhizines and seem to be closely related each other morphologically as well as chemically. These species are tentatively called the *P. physcioides* group for the purpose of this paper. Although species belonging to this group contain atranorin and barbatic acid in common, the secondary products accompanying these two substances are quite variable. In the present paper, the variation in secondary products found in these species is reported. Unfortunately, *P. steyermarkii* Hale, a South American species with ciliate lobules, has not been included in the present paper as no material was available for study.

Materials and method Two hundred and one specimens belonging to the *P. physcioides* group preserved in TNS were examined morphologically and

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chemically. As with other groups of *Parmelia*, the present species group includes sorediate (25 specimens), pustulate (86 specimens) and isidiate (50 specimens) morphs and a morph with no vegetative propagules (40 specimens; abbreviated as NVP in this paper). The chemical constituents present in each specimen were identified by comparison with authentic samples on thin layer chromatograms developed with a mixture of *n*-hexane, ethyl ether, and formic acid (5: 4: 1). Using this method, the known substances eluted in the following sequence from highest to lowest Rf atranorin, barbatic acid,. obtusatic acid, 4-0-demethylbabrbatic acid, norobtusatic acid, conechinocarpic acid, echinocarpic acid.

Results Eight of the nine compounds detected with TLC occur in biosequentially related pairs of substances. These pairs included 1) obtusatic and norobtusatic acids, 2) barbatic and 4-0-demethylbarbatic acids, 3) conechinocarpic and echinocarpic acids, and 4) fumarprotocetraric and succinprotocetraric acids. In the first two pairs the individuals differ only in that one depside is 0-methylated at the 4-hydroxy group, while the other is not and are consequently closely related biosynthetically (Culberson & Hale 1973). Similar as conechinocarpic acid usually accompanies echinocarpic acid (Culberson & Hale 1973) one can also presume that these two substances are closely related, although their chemical structure has yet to be elucidated. Similarly succinprotocetraric acid often accompanies fumarprotocetraric acid (Baker et al. 1973) and these two depsidones are closely related structurally as well as biosynthetically. On rare occasions failure to detect one member of a typically co-occurring pair of substances can probably be considered to result from low concentration rather than true absence, following Culberson & Hale (1973). On the other hand, atranorin was demonstrated in all specimens tested. It is a common substance produced in the cortex of lichen thallus and is also found in many other species and genera. Since it does not seem to have any taxonomic significance in this species group, it is excluded from the following discussion.

Tab. 1 summarizes the correlation between the major morphological characters and chemical combinations observed in the *P. physcioides* group. Most of the possible combinations of morphological characters (NVP, sorediate, pustulate, and isidiate) are observed within each chemotype of the *P. physcioides* group. In the past, a number of species names have been given to taxa with certain combinations of morphological and chemical characters: *P. physcioides* to the

Tab. 1. Chemical and morphological data for the *P. physcioides* group.

chemical race	obtusatic / norobtusatic	barbatic / 4-0-demethylbarbatic	conechinocarpic / echinocarpic	fumarprotocetraric / succinprotocetraric	morphological characters			
					NVP	sorediate	pustulate	isidiate
I		+			*P. ducalis* *P. massartii*		*P. exsecta*	*P. orientalis*
II		+	+		*P. scytodes*		*P. adjuncta* I	*P. addita* I
III		+		+			*P. adjuncta* II	*P. addita* II
IV	+	+			*P. physcioides*	*P. laevigata*	*P. virginica* unnamed	*P. imbricatula*
V	+	+	+		unnamed	unnamed	unnamed	*P. dentella* unnamed

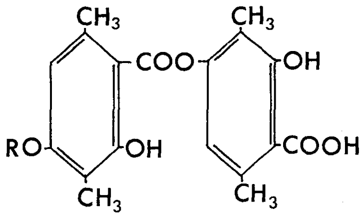
combination of NVP and chemical race IV, *P. exsecta* Tayl. to that of pustulate and chemical race I, etc. (Tab. 1). However, no names have been given to taxa exhibiting some combinations of characters such as that of NVP and chemical race V, of sorediate and chemical race V, etc. On the other hand, the following combinations have not been observed among the specimens examined. These include the following combination of characters: NVP and chemical race III, sorediate and chemical race I, sorediate and chemical race II, sorediate and chemical race III, and isidiate and chemical race III. However, the last combination was reported as *P. addita* II by Culberson & Hale (1973).

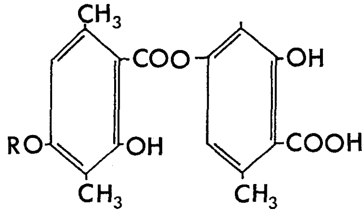
Discussion In all sorediate specimens, obtusatic, norobtusatic, barbatic, and 4-0-demethylbarbatic acids were clearly demonstrated so that these substances can be considered to be constant secondary products. Conechinocarpic acid and echinocarpic acid were detected in eight of 25 sorediate specimens, though their concentration was very variable. In particular conechinocarpic acid could only be detected in trace amounts in four of the eight specimens. Because of the low concentrations involved it was occasionally very difficult to distinguish specimens of chemical race V and chemical race IV. More relevant was the fact that the presence or absence of echinocarpic acid and conechinocarpic acid appeared to have no correlation with the morphology or distribution of the

lichens concerned. These substances, therefore, are best considered as biogenetically distant accessory compounds (Elix 1982), which occur sporadically in the species, *P. laevigata*.

In the NVP specimens, representatives belonging to the chemical races I, II, IV, and V were found. Actually two species having NVP and belonging to chemical race I have been recognized, namely *P. ducalis* Jatta (Krog & Swinscow 1979) and *P. massartii* Hue. Although only one specimen of *P. ducalis* has been examined (an isolectotype of *P. subplumbeata* Dodge), this species appears to be distinguished from *P. massartii* by the strongly maculate upper surface of the lobes. This morphological distinction was discussed previously by Hale (1975) under *Hypotrachyna subplumbeata* (Dodge) Hale. Although *P. scytodes* Kurok. belongs to chemical race II, the lobes are not maculate and are quite similar to those of *P. massartii*. In *P. scytodes*, the concentration of conechinocarpic acid and echinocarpic acid is quite variable, and as was the case with *P. laevigata*, the presence or absence of these two substances does not seem to be of any taxonomic significance. In other words, *P. massartii* and *P. scytodes* can be considered to be synonymous and to be alternative chemical races of the one species. A similar relationship was also found between the combination of NVP and chemical race IV (*P. physcioides*) and that of NVP and chemical race V (unnamed). Thus, the chemical race V, which is reported here for the first time, can be simply regarded as a chemical variant of *P. physcioides*.

In the combinations of NVP and chemical race IV and of NVP and chemical race V, obtusatic and norobtusatic acids are present in addition to barbatic and 4-0-demethylbarbatic acids. In these chemotypes, the concentration of obtusatic and norobtusatic acids is variable, whereas barbatic and 4-0-demethylbarbatic acids can readily be detected in all specimens. Thus of the 18 specimens examined belonging to chemical race IV, obtusatic acid could not be detected in four specimens and only traces could be demonstrated in two others. Further, norobtusatic acid could not be detected in one of 18 specimens, and was only present in trace quantities in four others. Similarly in the 9 specimens of chemical race V, obtusatic acid was present only in traces in two specimens, and norobtusatic acid in one. Indeed in most specimens of chemical races IV and V, obtusatic acid and norobtusatic acid were usually present in low concentration by comparison with barbatic and 4-0-demethylbarbatic acids. Pre-



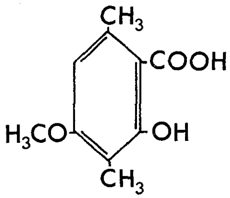


BARBATIC R= CH_3

4-0-DEMETHYLBARBATIC R= H

OBTUSATIC R= CH_3

NOROBTUSATIC R= H



RHIZONIC

Fig. 1. Comparison of molecular structures of barbatic, 4-0-demethylbarbatic, obtusatic, norobtusatic, and rhizonic acids.

viously the presence or absence of obtusatic and norobtusatic acids has been considered to be of taxonomic significance, and indeed the morphologically similar species, *P. massartii*, *P. scytodes*, and *P. physcioides*, have been distinguished in this way (Culberson & Hale 1973, Hale 1979).

Barbatic and 4-0-demethylbarbatic acids are *para* β-orcinol depsides, while obtusatic and norobtusatic acids are mixed *para* orcinol-β-orcinol depsides (Fig. 1). Structurally barbatic acid comprises a rhizonic acid unit (=4-0-methyl-β-orcinolcarboxylic acid) (Fig. 1) and a β-orcinolcarboxylic acid unit. The joint occurrence of rhizonic acid and barbatic acid in *P. subnuda* Kurok. (Kurokawa & Elix 1971) strongly suggests that 0-methylation at the 4-hydroxy group takes place before the formation of the depside linkage. Nonetheless, barbatic and 4-0-demethylbarbatic acids are primarily derived from β-orcinolcarboxylic acid units, while obtusatic and norobtusatic acids are derived from a β-orcinolcarboxylic acid unit and an orsellinic acid unit. The enzyme or enzymes responsible for the biosynthesis of the orsellinic acid precursor must be present in individuals producing obtusatic and/or norobtusatic acids. However, since barbatic acid

and 4-0-demethylbarbatic acid are produced in all the chemical races, the enzyme or enzymes responsible for the biosynthesis of the β-orcinolcarboxylic acid precursors must be constantly present (this unit is also required for the production of obtusatic acid and norobtusatic acid). The fact that the concentrations of obtusatic and norobtusatic acids are variable suggests that the activity (or even presence or absence) of enzymes catalizing the steps in the biosynthesis of orcellinic acid unit is not constant (or perhaps stable).

In section Hypotrachyna, there is a group of species which produce evernic and lecanoric acids. Morphologically these species closely resemble the *P. physcioides* group. Both evernic (=4-0-methyllecanoric acid) and lecanoric acids are *para* orcinol depsides, where both rings are derived from an orsellinic acid unit (which also comprises ring B of obtusatic acid and norobtusatic acid). Culberson & Hale (1973) postulated that a hypothetical progenitor could have evolved by the hybridization of a fertile or NVP progenitor producing barbatic and 4-0-demethylbarbatic acids and one producing evernic and lecanoric acids. This might constitute a plausible evolutionary pathway to account for the joint four acids in chemical races IV and V of the NVP morph. As discussed above, however, the concentration of obtusatic and norobtusatic acids is quite variable and on occasions they appear to be absent from some specimens of the chemical races IV and V. In other words, the production of obtusatic and norobtusatic acids is not a stable character, and apart from the case of *P. ducalis*, may have little taxonomic significance in the NVP morph. In conclusion, conechinocarpic acid and echinocarpic acid as well as obtusatic and norobtusatic acids are considered to be accessory components and the presence or absence is regarded only as a minor chemical variation within the one species, *P. physcioides*.

The name *P. virginica* Hale has been proposed for one of the pustulate morph of this species group. *P. virginica* is endemic to eastern North America, and like *P. ducalis*, it is distinctly maculate on the upper surface of lobes. Chemically it has been shown to belong to chemical race IV. The thallus is distinctly wrinkled on the upper surface and pustules are usually formed along the ridges of wrinkles. These pustules often extend along the ridges to form irregular pustular masses (Hale & Kurokawa 1964). A different pustulate morph has now been discovered with 14 specimens from southeastern Asia and Papua New Guinea. This taxon also belongs to chemical race IV, but in these specimens pustules are formed near the apices of lobes and are rounded, and the

upper surface is smooth and emaculate (as observed in the pustulate specimens belonging to the alternative chemical races). Although this taxon has not been previously named (Tab. 1), it appears to be related to *P. exsecta* (chemical race I) and *P. adjuncta* Hale (chemical race II). *P. virginica*, on the other hand, is not closely related to the other pustulate morphs.

In the pustulate and isidiate morphs, all chemical races are represented. The chemical variation shown by the chemical races I, II, IV, and V of these two morphs are quite similar to those described for NVP morph. Barbatic and 4-0-demethylbarbatic acids are the constant, major components. Obtusatic and/or norobtusatic acids were demonstrated in the chemical races IV and V and conechinocarpic acid and/or echinocarpic acid were found in the chemical races II and V. As was the case for the NVP morph discussed above, these two pairs of substances can be considered to be accessory components in pustulate and isidiate morphs, respectively, although their concentration seems to vary independently.

A specimen which has been identified as *P. adjuncta* (Kashiwadani 1819 collected in Papua New Guinea) has been found to contain succinprotocetraric acid and fumarprotocetraric acid in addition to barbatic and 4-0-demethylbarbatic acids. The former substance has not previously been reported as occurring in the *P. physcioides* group. The taxonomic significance of succinprotocetraric and fumarprotocetraric acids has not been fully studied. However, these two acids may be biosynthetically closely related to echinocarpic acid, which is related to the postulated depside precursor of the protocetraric acid-type depsidones (Culberson & Hale 1973). They are tentatively regarded as accessory components related to conechinocarpic acid and echinocarpic acid in the present study. Fumarprotocetraric acid has also occasionally been observed in *P. addita* Hale (*P. addita* II in Tab. 1), another isidiate morph (Culberson & Hale 1973).

Most isidiate specimens belonging to chemical race V are morphologically identical with the other isidiate specimens of alternative chemistry. However, *P. dentella* Hale et Kurok. is distinctly white-maculate on the upper surface of lobes. This species is also chemically unique since obtusatic acid is the major secondary metabolite present, together with minor amounts of barbatic and norobtusatic acids. 4-0-Demethylbarbatic acid could not be detected in this species. Thus, *P. dentella* appears to be a distinctive species of different origin, which is not closely related to the other isidiate species of the group. So

apart from the maculate species, *P. virginica* and *P. dentella,* five chemical races with various combinations of four pairs of substances can be recognized in the pustulate and isidiate morphs, and all are considered to be chemical variants of *P. exsecta* and *P. imbricatula.*

Apart for the production of fumarprotocetraric and succinprotocetraric acids, the NVP, pustulate, and isidiate morphs show identical chemical variations as discussed above. These morphs represented by *P. physcioides, P. exsecta,* and *P. imbricatula* respectively, are considered to be closely related each other in morphology as well as in chemistry, although *P. ducalis, P. virginica,* and *P dentella* should be excluded from this group on the basis of their distinctive morphologies discussed above.

In 1970, Poelt summarized many examples of species pairs (Artenpaare) in lichens consisting of a primary sexual species without vegetative propagules and secondary or asexual species with vegetative propagules. Briefly, he postulated that the asexual sorediate and isidiate morphs are derived from sexual progenitors. Later, he (Poelt 1972) expanded this hypothesis to include the differentiation of a parent species into two or more chemically different sexually reproducing species, each of which could produce stable secondary apomictic species. The *P. physcioides* group seems to represent a good example of Poelt's hypothesis. As already mentioned, the NVP, pustulate, and isidiate morphs show parallel chemical variations. The pustulate and isidiate morphs can be considered to have been differentiated from the NVP morph (excluding *P. ducalis*), by the acquisition of asexual propagules such as pustules or isidia, but retaining identical chemical variations (Fig. 2). In other words, the pustulate morph, *P. exsecta,* and the isidiate morph, *P. imbricatula,* are considered

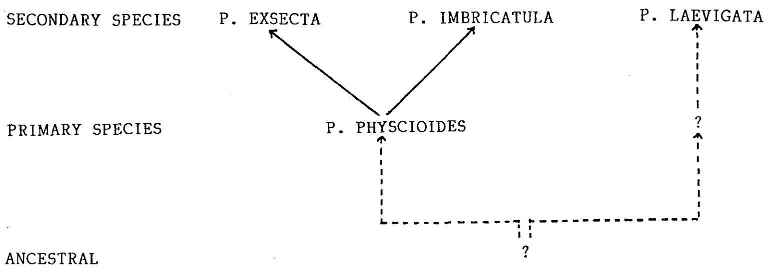


Fig. 2. Hypothetical evolution of the species of the *Parmelia physcioides* group.

to be derived from the parent NVP morph, *P. physcioides*. In contrast, the sorediate morph, *P. laevigata*, exhibits different chemical variations in lacking chemical races I and II. Even though *P. laevigata* resembles the NVP morph *P. physcioides* morphologically, it seems to have been derived from a different sexual ancestor, in which obtusatic and norobtusatic acids as well as barbatic and 4-0-demethylbarbatic acids were constantly produced (Fig. 2). Thus in the strict sense the sorediate morph, *P. laevigata*, does not seem to form a pair with any of the presently known NVP morphs. The remaining three species, *P. ducalis*, *P. virginica*, and *P. dentella*, are distinguished in having a maculate upper surface of lobes and are restricted in distribution to the Western Hemisphere. These facts seem to indicate that these three species are closely related. However, they show quite different chemical features as already mentioned and the evolutionary relationships between them are not clearly known at present.

Parmelia dentella Hale et Kurok., Contr. U.S. Nat. Herb. **36**: 172, 1964.

Hypotrachyna dentella (Hale et Kurok.) Hale, Smiths. Contr. Bot. **25**: 33, 1975.

Chemical substances. Atranorin, barbatic acid, 4-0-demethylbarbatic acid(?), obtusatic acid, norobtusatic acid, conechinocarpic acid, and echinocarpic acid.

Distribution. Southeastern United States, Mexico, Venezuela, and Brazil.

Parmelia ducalis Jatta, Ann. Bot. **6**: 407, 1908.

Parmelia subplumbeata Dodge, Ann. Miss. Bot. Gard. **56**: 106, 1959—*Hypotrachyna subplumbeata* (Dodge) Hale, Smiths. Contr. Bot. **25**: 67, 1975.

Hypotrachyna ducalis (Jatta) Hale, Smiths. Contr. Bot. **25**: 33, 1975.

Chemical substances. Atranorin, barbatic acid, and 4-0-demethylbarbatic acid.

Distribution. Mexico and Africa.

Parmelia exsecta Tayl., London Journ. Bot. **6**: 166, 1847.

Parmelia laevigata f. *esorediata* Zahlbr., Bot. Mag. Tokyo **41**: 351, 1927.

Parmelia laevigata subsp. *extremi-orientalis* Asah., Journ. Jap. Bot. **26**: 289, 1951.

Parmelia adjuncta Hale, Phytologia **22**: 434, 1971—*Hypotrachyna adjuncta* (Hale) Hale, Phytologia **28**: 340, 1974. Syn. nov.

Hypotrachyna exsecta (Tayl.) Hale, Phytologia **28**: 341, 1974.

Chemical substances. Atranorin, barbatic acid, 4-0-demethylbarbatic acid, obtusatic acid (+ or −), norobtusatic acid (+ or −), conechinocarpic acid

(+ or −), echinocarpic acid (+ or −), fumarprotocetraric acid (+ or −), and succinprotocetraric acid (+ or −).

Distribution. Southeastern and eastern Asia and southern Pacific, including Australia.

Parmelia imbricatula Zahlbr., Denkschr. Akad. Wiss. Wien Math.-Naturwiss. Kl. **83**: 168, 1909.

Parmelia addita Hale, Phytologia **22**: 433, 1971—*Hypotrachyna addita* (Hale) Hale, Phytologia **28**: 340, 1974. Syn. nov.

Parmelia orientalis Hale, Phytologia **22**: 435, 1971—*Hypotrachyna orientalis* (Hale) Hale, Phytologia **28**: 341, 1974. Syn. nov.

Hypotrachyna imbricatula (Zahlbr.) Hale, Smiths. Contr. Bot. **25**: 41, 1975.

Chemical substances. Atranorin, barbatic acid, 4-0-demethylbarbatic acid, obtusatic acid (+ or −), norobtusatic acid (+ or −), conechinocarpic acid (+ or −), echinocarpic acid (+ or −), and fumarprotocetraric acid (+ or −).

Distribution. Widely distributed in tropical and subtropical areas.

Parmelia laevigata (Sm.) Ach., Syn. Lich. 212, 1814.

Lichen laevigatus Sm., Eng. Bot. **26**: 1852, 1808—*Hypotrachyna laevigata* (Sm.) Hale, Smiths. Contr. Bot. **25**: 44, 1975.

Chemical substances. Atranorin, barbatic acid, 4-0-demethylbarbatic acid, obtusatic acid, norobtusatic acid, conechinocarpic acid (+ or −), and echinocarpic acid (+ or −).

Distribution. United States southward to Chile, Europe, and Africa.

Parmelia physcioides Nyl., Syn. Lich. 385, 1860.

Parmelia massartii Hue, Nouv. Arch. Mus. Paris, ser. 3. **1**: 168, 1899—*Hypotrachyna massartii* (Hue) Hale, Phytologia **28**: 341, 1974. Syn. nov.

Parmelia bostrychodes Zahlbr., Ann. Crypt. Exot. **1**: 203, 1928—*Hypotrachyna bostrychodes* (Zahlbr.) Hale, Phytologia **28**: 340, 1974. Syn. nov.

Parmelia scytodes Kurok. in Hale & Kurokawa, Contr. U. S. Nat. Herb. **36**: 185, 1964—*Hypotrachyna scytodes* (Kurok.) Hale, Phytologia **28**: 341, 1974. Syn. nov.

Hypotrachyna physcioides (Nyl.) Hale, Smiths. Contr. Bot. **25**: 54, 1975.

Chemical substances. Atranorin, barbatic acid, 4-0-demethylbarbatic acid, obtusatic acid (+ or −), norobtusatic acid (+ or −), conechinocarpic acid (+ or −), and echinocarpic acid (+ or −).

Distribution. Southeastern Asia, southern Pacific, and tropical America.

Parmelia virginica Hale in Hale & Kurokawa, Contr. U. S. Nat. Herb. **36**: 186, 1964.

Hypotrachyna virginica (Hale) Hale, Phytologia **28**: 342, 1974.

Chemical substances. Atranorin, barbatic acid, 4-0-demethylbarbatic acid, obtusatic acid, and norobtusatic acid.

Distribution. Endemic to eastern North America.

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Explanation of Plate III

Fig. 1. *Parmelia physcioides* Nyl. (Sipman 12408 collected in Costa Rica). ×0.8. Fig. 2. *Parmelia laevigata* (Sm.) Ach. (Kashiwadani 18250 collected in Chile). ×0.9. Fig. 3. *Parmelia exsecta* Tayl. (Kurokawa 60160 collected in Japan). ×0.8. Fig. 4. *Parmelia imbricatula* Zahlbr. (Kurokawa 9320 collected in Papua New Guinea). ×0.8.

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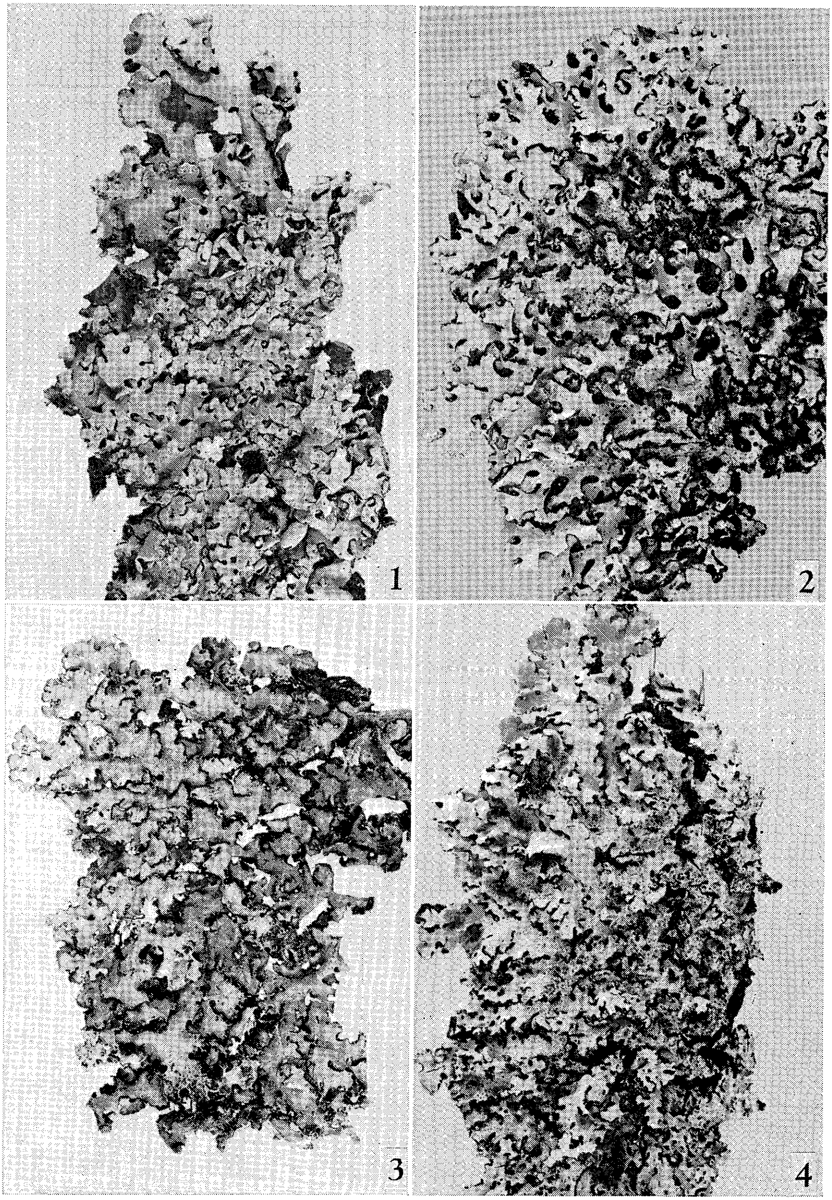
ウメノキゴケ属の1群で，熱帯，亜熱帯に広く分布する *Parmelia physcioides* 群に含まれる12種について，その二次代謝産物の変異を調べた。これらの種にはアトラノリンとバルバチン酸のほかに1～5の別の二次代謝産物が含まれていて，様々な変異を示す。一方，形態的には無性生殖器官のないもの (NVP) と粉芽，裂芽，パスチュールなどの無性生殖器官をもつものがある。これらのうち *P. ducalis* (NVP)，*P. virginica*（パスチュールあり），*P. dentella*（裂芽あり）の3種は形態的にも特徴があり，別の種群に属することを示した。また，粉芽をもつ *P. laevigata* は化学的にも異なった性質をもつので，厳密な意味での *P. physcioides* 群から除いた。その他の8種は，それぞれ *P. physcioides* (NVP)，*P. exsecta*（パスチュールあり），*P. imbricatula*（裂芽あり）の何れかに属する単なる化学的変異体とみなされることを示した。

○帰化植物フジボツルハギ（大橋広好） Hiroyoshi OHASHI: A record of *Desmodium intortum* (Leguminosae) naturalized in Japan

沖縄にフジボツルハギと名付けられたマメ科の一種が帰化している。多和田真淳監修，池原直樹：沖縄植物野外活用図鑑，第3巻　帰化植物 64-65ページ（1979年）に花の時期の美しい写真が載せられている。これまでこの植物の学名に *Dioclea violacea* Mart. が用いられているが，正しくはヌスビトハギ属のものであり，中南米の熱帯，亜熱帯地方に原産する *Desmodium intortum* (Mill.) Urb. あるいは *D. uncinatum* (Jacq.) DC. に当たるものである。

Desmodium intortum あるいは *D. uncinatum* とするのは不正確のようであるが，これには次のような事情がある。これらの種は分布が広く，外部形態上の変異が著しいため，形態的に似た多くの種類が記載されている。1926年には，ヌスビトハギ属の専門家であった A.K. Schindler 博士が *D. intortum, D. uncinatum* およびその近縁種について研究し，11種を認めたが，しかし，両種はもとより，これらの近似の種の特徴が充分に捕らえられておらず，個々の種が分類学的に明瞭に区別されなかった。この結果は，細分しすぎてかえって混乱をまねいてしまっている。今日では似た種類が集められて *D. intortum-uncinatum* complex と総括されているが，この complex をどのように正しく分類するのか解決されておらず，中南米のヌスビトハギ属分類の難問題の1つとなっている。この complex の中で，特に，*D. intortum, D. uncinatum,* および，同じく中南米の種である *D. aparines* および *D. limense* の4種の異同について見解が別れている。これらの4種は同一種であるとする Fosberg (1968) の見解に従えば，フジボツルハギは *D. intortum* (Mill.) Urb. に当る。しかし，Schindler や Schubert



S. KUROKAWA: *Parmelia physcioides* group